
A NEW BROODING BRITTLE STAR FROM CALIFORNIA (ECHINODERMATA: OPHIUROIDEA: AMPHIURIDAE)

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ABSTRACT. *Amphiodia akosmos* n. sp. is the only *Amphiodia* species known to bear live young, and like many brooding brittle stars, it is of diminutive size. It is characterized by irregularly arranged opaque disk scales, primary disk plates that are inconspicuous or lacking, wing-shaped middle arm spines, and a single elongate tentacle scale. There is an allometric relationship between arm length and disk diameter. Specimens of different sizes cannot be characterized by a unique ratio of arm length to disk diameter, a complication generally ignored in previous descriptions of ophiuroids. Adult individuals attain approximately 4 mm disk diameter and closely resemble the young of a larger, sympatric species, *Amphiodia occidentalis*. This suggests that *A. akosmos* is progenetic. However, various of its characteristics may be pedomorphic, peramorphic, and nonheterochronic in origin. In contrast to female *A. occidentalis*, which broadcast-spawn thousands of small eggs, *A. akosmos* individuals hold fewer than 30 yolky eggs, which can reach 430 μ m in diameter. All dissected specimens (N = 8) were female, an indication that the species could be gonochoric, but also that it might be protandric or parthenogenetic. Thus far, the species is known only from the intertidal zone within 200 km of the Monterey Peninsula, California.

INTRODUCTION

"It is a fabulous place: when the tide is in, a wave-churned basin, creamy with foam, whipped by the combers that roll in from the whistling buoy on the reef. But when the tide goes out the little water world becomes quiet and lovely. The sea is very clear and the bottom becomes fantastic with hurrying, fighting, feeding, breeding animals. . ." (Steinbeck, 1945)

From time to time, an unnamed species of *Amphiodia* has been recognized as inhabiting the central California coast. It is named and described herein, based primarily on specimens collected from the Great Tide Pool, at Point Piños, on the tip of the Monterey Peninsula, the locality vividly depicted in the epigraph.

That naming this species has been so long delayed, despite its having been noted in two editions of *Light's Manual* (Weesner, 1954; Sutton, 1975), is indicative of the scant attention that has been directed toward Eastern Pacific ophiuroids. Although the first account of the fauna was published over 150 years ago (Müller and Troschel, 1843), Eastern Pacific ophiuroids have never been extensively collected, their representation in museums is limited, and the group has not been monographed. The present study is a small step toward correcting that situation.

Friedman (1948) may have been the first to no-

tice the new species. He reported two specimens, which were from Monterey Bay, of *Amphiodia* with "one broad tentacle scale" and a disk diameter of about 2 mm. Although he mistakenly identified them as a tropical species, his description of the animals suggests that he had found either the new species reported herein, or juvenile individuals of *Amphiodia occidentalis* (Lyman, 1860). Although some of Friedman's ophiuroids are deposited at the California Academy of Sciences, these specimens of "*Amphiodia tabogae*" are believed lost.

The new species was certainly known to Weesner (1954), who differentiated "*Amphiodia* sp." from *A. occidentalis* in the second edition of *Light's Manual*. She distinguished the new species based on its arm/disk ratio and single tentacle scales, and more definitively by its "ovoviviparous" reproduction. Unfortunately, no record exists of where along the central California coast her specimens were collected (F. Lechleitner, née Weesner, personal communication).

The second author of the present report (under the name Cunningham, 1977) rediscovered the small, brooding *Amphiodia* species in the course of research on *A. occidentalis*. She noted additional features distinguishing the two *Amphiodia* species, in addition to those taxonomic characters cited by Weesner (1954). Specimens that she collected were examined by Sutton (1975) and treated as "*Amphiodia* sp." in the third edition of *Light's Manual*. However, as noted below, Sutton evidently confused juvenile *A. occidentalis* and adults of the new species and incorrectly concluded that the new species "May be a variety of *A. occidentalis*" (Sutton,

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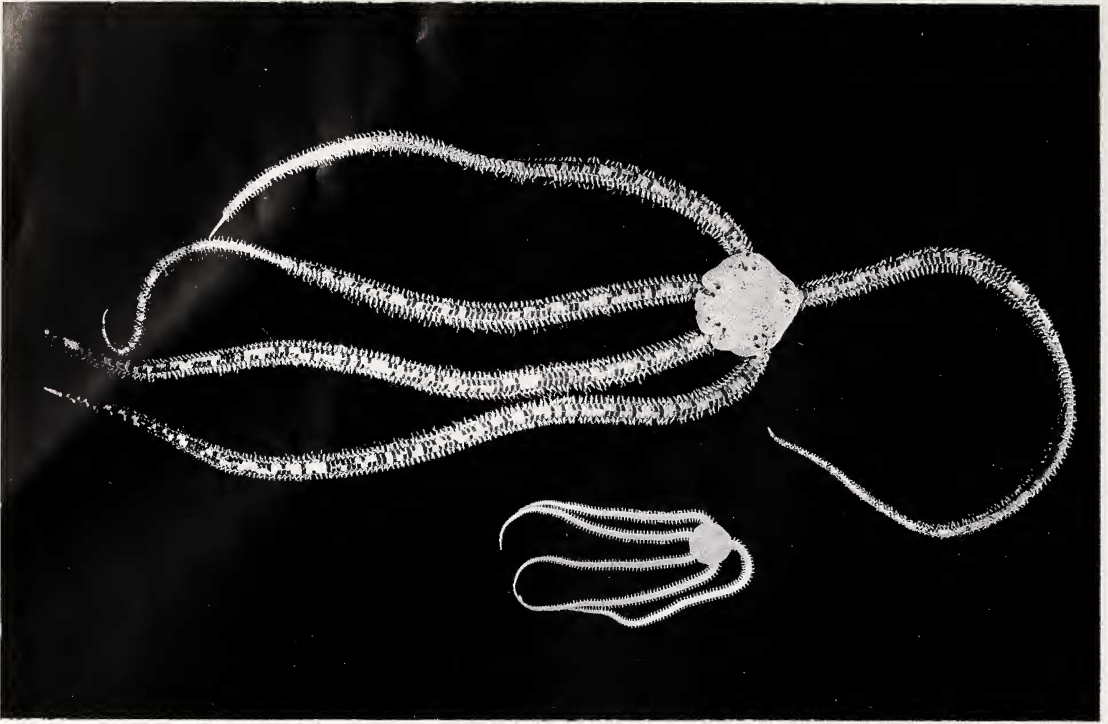


Figure 1 *Amphiodia occidentalis*, 8.1 mm dd, LACM 1998-089.010 (top), an adult individual of moderate size; *Amphiodia akosmos*, 3.5 mm dd, holotype, LACM 1993-035.004 (bottom), a full-grown adult

1975:633). Until this report, nothing further was published on the species, save for references to Cunningham's observations (Austin and Hadfield, 1980; Rumrill and Pearse, 1985; Hendler, 1991).

MATERIALS AND METHODS

Standard methodology and terminology were used for the taxonomic analysis. The diameter of the disk (dd) was measured from the outer edge of the radial shields to the opposite edge of the disk. The length of the arm (AL) was measured for the longest arm of an individual, from the edge of the disk to the arm tip. Data were not recorded for specimens with broken or regenerated arms.

The AL and dd of a range of sizes of *A. occidentalis* from several localities were measured for comparison with individuals of the new species. The allometric equation, $Y = aX^b$ (where $Y = AL$, $X = dd$), was used to describe the relationship between arm and disk dimensions. Statistical analysis of the data was based on a Model I regression of the linearized expression, $\ln Y = \ln a + b \ln X$. Two-tailed Student's *t* tests were used to determine the significance of the regression based on deviation of the correlation coefficient from zero, and departure from isometry based on deviation of the regression coefficient (= constant of allometry) from unity (Sokal and Rohlf, 1995).

The following abbreviations are used in this paper. CASIZ, California Academy of Sciences; LACM, Natural History Museum of Los Angeles County; USNM, National Museum of Natural History.

SYSTEMATIC ACCOUNT

Family Amphiuridae

Genus *Amphiodia* Verrill, 1899

Amphiodia (*Amphiodia*) *akosmos* new species Figures 1–4

Amphiodia sp. Weesner, 1954:291; Sutton, 1975:631, in part; Cunningham, 1977:41.

ETYMOLOGY. The specific name, transliterated from the Greek term for "unorganized," refers to the irregular distribution of dorsal disk scales and to the apparent absence of the rosette of primary disk plates that comprise an orderly system ("kosmos") in other species of *Amphiodia*.

MATERIAL EXAMINED. Except as noted, all specimens in the type series are preserved in ethanol and were collected from the intertidal zone in the Great Tide Pool at Point Piños, Pacific Grove, Monterey County, California, located approximately 36° 37.7'N, 121° 56.20'W.

Holotype. (LACM 1993-35.4), 24 Jul. 1993, coll. Hendler.

Paratypes. (LACM 1976-659.1), 1 spec., brooding, 16 Feb. 1976, coll. Bundrick; (LACM 1975-674.1), 1 spec., 7 Oct. 1975, coll. Bundrick; (LACM 1975-674.2), 1 spec., 7 Oct. 1975, coll.

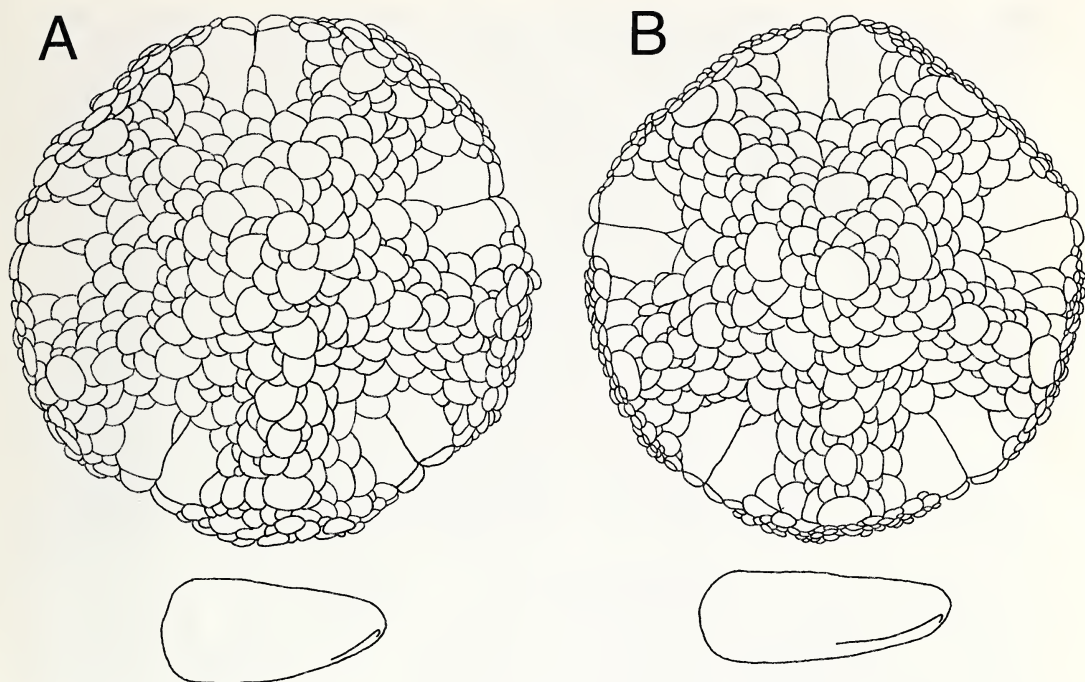


Figure 2 Dorsal view of the disk and the middle spine on the 10th arm joint from the disk edge of: A, adult *Amphiodia akosmos*, holotype, LACM 1993-035.004, 3.5 mm dd, spine length 0.28 mm; B, juvenile *Amphiodia occidentalis*, LACM, 1993-036.007, 3.4 mm dd, spine length 0.32 mm

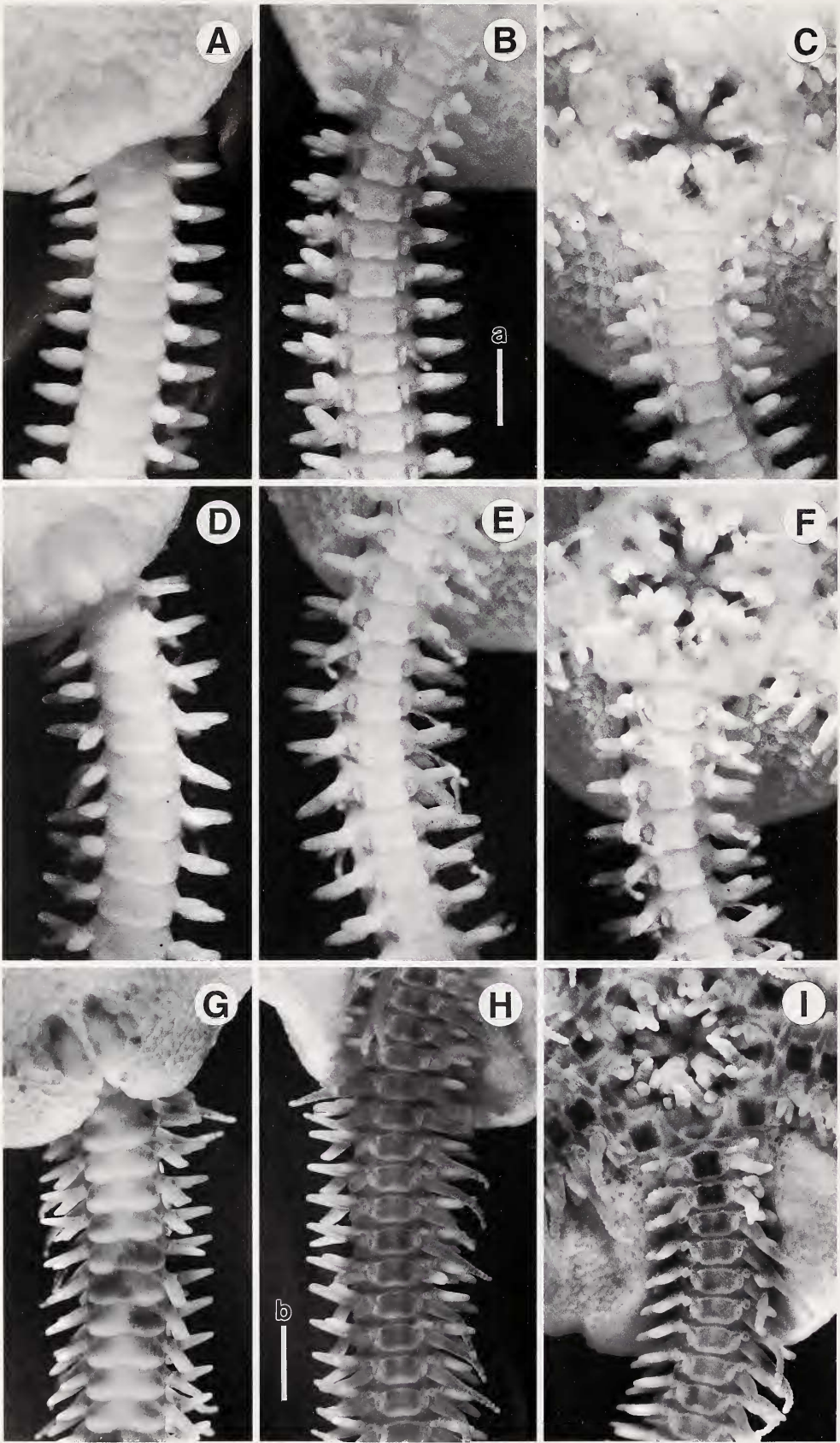
Bundrick; (LACM 1975-675.1), 2 spec., 3 Nov. 1975, coll. Bundrick; (LACM 1993-36.2), 3 spec., 23 July 1993, coll. Hendler and Bundrick; (LACM 1993-036.6), 1 spec., 23 July 1993, coll. Hendler and Bundrick; (LACM 1993-35.1), 2 spec., 24 July 1993, coll. Hendler; (LACM 1999-48.1), 1 spec., 27 Mar. 1999, coll. Bundrick; (USNM E51873), 1 spec., brooding female, 24 Oct. 1999, coll. Bundrick; (LACM 1999-49.2), 1 spec., female, 24 Oct. 1999, coll. Bundrick; (LACM 1999-49.3), 1 spec., female, 24 Oct. 1999, coll. Bundrick; (LACM 1999-50.1), 1 spec., female, 21 Nov. 1999, coll. Bundrick; (LACM 1999-50.2), 1 spec., female, 21 Nov. 1999, coll. Bundrick; (LACM 1999-051.1), 1 spec., female, 7 Dec. 1999, coll. Bundrick; (LACM 2000-1.1), 1 spec., brooding female, 19 Feb. 2000, coll. Bundrick; (LACM 2000-1.2), 1 spec., brooding female, 19 Feb. 2000, coll. Bundrick; (CASIZ 1238), 1 spec., 3 Jun. 1973, coll. Nakashima; (CASIZ 9550), 1 spec., Jewell Cave, Southeast Farallon Island, intertidal, 30 Aug.–2 Sep. 1975, coll. Chaffee, Lindberg; (CASIZ 15733), 2 spec., Hopkins Marine Station, 1921, coll. Wallace.

DIAGNOSIS. Adult body size small; dd 2.0–4.2 mm; AL 9.6–23.8 mm (Fig. 1). Dorsal disk scales irregularly arranged, primary plates inconspicuous or lacking, boundary between dorsal and ventral disk scales not sharply demarcated (Figs. 2, 3). Radial shields nearly semicircular, width of peripheral

scale capping its distal edge equals or exceeds one-half width of the shield. Ventral arm plate subpentagonal; distal edge longest, with medial indentation forming two distolateral lobes. Three erect arm spines; dorsal and ventral spines proximodistally compressed, with bluntly rounded or flared tip; middle spine wing-shaped in dorsal view, base triangular in cross section with dorsoventrally compressed distal edge forming keel, outer portion of spine proximodistally compressed, ovoid to rounded in cross section, with tapering to bluntly rounded tip. Tentacle scale single, elongate, ovoid to bilobate; scale length on arm joints beneath disk approximately one-half that of associated ventral arm plate.

DESCRIPTION OF HOLOTYPE. Disk diameter 3.3 mm; AL 16.8 mm.

Disk. Rounded pentagonal, lacking mid-interradial notches, covered by irregularly arranged, imbricating scales; boundary between dorsal and ventral disk scales not sharply demarcated by closely aligned marginal scales. Primary plates inconspicuous or lacking. Scales opaque, somewhat irregularly shaped, with rounded edges; largest in dorsal interradian region, smallest in ventral interradian. Genital scales inconspicuous, tilting into bursal slit, appearing similar in size to ventral interradian scales. Bursal slit extending from near posterior margin of oral shield almost to edge of disk.



Radial Shield. Nearly semicircular, narrowing proximally, with broad, straight distal end; length equaling approximately one third of disk radius. Peripheral scale capping distal end of radial shield, subquadrate, thick, width equaling or exceeding one-half width of radial shield. Paired radial shields in contact distally; proximal ends separated by broad wedge-shaped scale, and frequently by narrow wedge-shaped scale distad.

Jaw. Narrow, with three, bluntly rounded oral papillae. Oral slits wide. Paired infradental papillae largest, blocklike, not markedly inflated, tapering distally, tilting upward toward teeth. Distal papillae erect, tabulate. Middle papilla smallest, elongate, with distal edge truncate, broader than base. Outer papilla elongate, with tapered, bluntly rounded distal edge.

Oral Shield. Rhombic, with bluntly rounded corners, width equaling or exceeding length. Proximal edges somewhat convex, longer than distal edges. Madreporite larger, rounder than oral shield; distal side expanded, convex, with single pore.

Adoral Shield. Long, narrow proximal lobe aligned with oral shield; short, distal lobe abutting first ventral arm plate. Paired shields touching within, or nearly so.

Arm. Constricted basally, gradually widening over approximately one-quarter total length, tapering to slender distal tip; broader than high in cross section; convex dorsally, flat ventrally.

Dorsal Arm Plate. Subhexagonal, twice as wide as long. Proximal edge convex; proximolateral edge meeting somewhat shorter posterolateral edge forming rounded projection; distal edge indented medially. Proximal plates slightly overlapping. Distal plates three-sided, separated by lateral arm plates, with straight obtusely angled proximal edges meeting at sharp apex, convex distal edge.

Lateral Arm Plate. Slender, with protruding articulation ridge. Dorsal side forming small, triangular wedge between dorsal arm plates, ventral side forming larger narrow wedge separating ventral arm plates. Successive plates joined by sheath of integument.

Ventral Arm Plate. Subpentagonal, width equaling or exceeding length. Proximal portion relatively thickened. Proximal edges somewhat concave, meeting at sharp obtusely angled apex; lateral edges convex, excavated to accommodate tentacle scale; distal edge longest, with medial indentation demarcating two distolateral lobes. Distal plates pentagonal, straight sided. First ventral arm plate inclining into oral slit, nearly perpendicular to ventral surface of disk; portion within oral slit, thin, narrow;

outer portion C-shaped, thickened, forming flat shelf between adoral shields.

Arm Spines. Erect, three in number (except two on first joint beneath disk); length of spines approximately equal, slightly less than width of ventral arm plate. At base of arm: dorsal spine proximodistally compressed, broader than thick, with somewhat concave distal side, outer tip bluntly rounded to flared; middle spine wing-shaped in dorsal view, base triangular in cross section, with distal edge dorsoventrally compressed, keel-shaped; outer portion of spine proximodistally compressed, ovoid to rounded in cross section, tapering to bluntly rounded tip; ventral spine resembling dorsal spine though less broad, narrower at outer tip, not distally concave. Spines increasing slightly in length from dorsal to ventral.

Tentacle Scale. Single, elongate, ovoid to somewhat bilobate; proximal end frequently slightly widened, inserted into angle between lateral and ventral arm plates; adradial edge aligned with excavated shelf on lateral edge of ventral arm plate; distal tip bluntly rounded. Length on arm joints beneath disk approximately one-half that of associated ventral arm plate.

Terminal Arm Plate. Strawberry shaped, with 0–2 sharp, minute protrusions at terminal pore.

Tube Foot. Shaft tapering, translucent; tip spheroidal, with two to four pairs of subterminal, ventrolateral, glandular bumps. Whitish in alcohol.

Color. Dorsally mostly whitish to pale beige; disk scales opaque, concealing dark brown stomach; some disk scales gray or brown, radial shields dark gray proximally, whitish distally; portions of some dorsal and lateral arm plates dark gray or black. Ventrally, some ossicles of oral frame pale gray, arm plates with whitish edges and traces of pale gray. Some proximal tube feet with pale yellowish pigmentation. All but gray and black coloration quickly lost in ethanol, most specimens fading to white.

Variation. The dd of available specimens, except embryos, ranges from 2.0–4.2 mm, AL from 13.3–23.8 mm and the AL/dd ratio from 5.0–6.9. Deviations from the holotype are manifested in the number of pores in the madreporite, which may be zero or one, the shape of the dorsal arm plates, which have a medial indentation in the holotype but lack a conspicuous notch in most other specimens, and the number of wedge-shaped scales separating the radial shields. Rarely, tips of ventral arm spines are flared, and basal ventral arm plates are separated by lateral arm plates. In the smaller specimens, length and width of second ventral arm plate are equal, buccal scales (*sensu* Hendler, 1978)

Figure 3 *Amphiodia akosmos* and *Amphiodia occidentalis*. A–C, adult *Amphiodia akosmos*, 3.5 mm dd, holotype, LACM 1993-035.004; D–F, juvenile *Amphiodia occidentalis*, 3.4 mm dd, LACM 1993-036.007; G–I, adult *A. occidentalis*, 8.1 mm dd, LACM 1998-089.010. For each specimen, shown from left to right are: the arm base and adjoining portion of the disk in dorsal view, the arm base and adjoining portion of the disk in ventral view, the oral frame and adjoining portions of disk and arm. Scale a = 0.5 mm (A–F); scale b = 1.0 mm (G–I)

Table 1. Features distinguishing adult *Amphiodia akosmos* from juvenile *Amphiodia occidentalis* of similar size (2.5–3.6 mm dd).

Species	<i>Amphiodia akosmos</i>	<i>A. occidentalis</i>
Disk scalation	Primary plates inconspicuous or lacking, scales irregularly arranged, opaque, relatively large; scales on dorsal and ventral sides not sharply demarcated at edge of disk	Primary plates conspicuous, scales symmetrically arranged, thin, relatively small; scales on dorsal and ventral sides sharply demarcated at edge of disk
Peripheral scale capping distal edge of radial shield	Width >½ width of radial shield	Width <½ width of radial shield
Wedge-shaped scales between radial shields	1–2 conspicuous scales; inner scale broad, outer scale slender	0–1 small scales
Arm spines	Robust	Relatively slender
Middle arm spine	Wing-shaped in dorsal view, with basal portion dorsoventrally compressed, forming a distal keel	Lacking a conspicuous distal keel
Second ventral arm plate	Width ≥ length	Width ≤ length
Infradental papilla	Inclined toward teeth	Perpendicular to dental plate
Oral shield	Width ≥ length	Width < length
Middle oral papilla	Truncate, broadest at distal tip	Bluntly rounded, broadest subterminally
Ventral arm plate	Distal edge bilobate, with medial indentation	Distal edge straight or slightly convex
Number of tentacle scales	1	0–2
Tentacle scale	Length >½ length of ventral arm plate	Length ≤½ length of ventral arm plate
Genital scale	Inconspicuous	Conspicuous

are present that are later resorbed, and the broad abradial edge of the radial shield is bare of scales. In some specimens the dorsal disk scales are pale brown and the outer tips of the arm spines are pale brown. Features of a newly emerged juvenile were considerably different from those of adults. It had five arm joints, which lacked tentacle scales, and its arms (0.46 mm) were shorter than the dd (0.67 mm).

COMPARISONS. A.M. Clark (1970) noted that only four of the nominal species in the subgenus *Amphiodia*, from east or west America, have three approximately equal oral papillae on each half of the jaw, as opposed to an enlarged operculate outer oral papilla. All except *Amphiodia pulchella* (Lyman, 1869) and *A. akosmos* have two tentacle scales. *Amphiodia pulchella* is readily distinguished from *A. akosmos* by its very finely scaled disk and slender radial shields.

Of the remaining eight species that are considered valid members of *Amphiodia* by A.M. Clark (1970), *Amphiodia euryaspis* H.L. Clark, 1911, must be referred to *Amphioplus* (see Sutton, 1976). The three congeners that, like *A. akosmos*, have equal oral papillae and a single tentacle scale are differentiated from it as follows. *Amphiodia acutispina* Koehler, 1914, has a thorny projection from the outer edge of the radial shield, and both *Amphiodia minuta* H.L. Clark, 1939, and *Amphiodia oblecta* Mortensen, 1940, have slender, acutely pointed arm spines. Two additional *Amphiodia*

species were described subsequent to A.M. Clark's (1970) monograph. *Amphiodia guillermosoberoni* Caso, 1979, is distinguished from *A. akosmos* by its paired tentacle scales and elongate, narrow radial shields. *Amphiodia picardi* Cherbonnier and Guille, 1978, has an *Amphioplus*-type oral formula and is probably an *Ophionephthys* species.

Distinctions Between Adults and Juveniles of *A. akosmos* and *A. occidentalis*. Despite their similarities, *A. akosmos* is readily distinguished from the much larger adult individuals of co-occurring *A. occidentalis* (Figs. 1, 3). *Amphiodia occidentalis* reaches 12 mm dd with AL/dd ratios of up to 18, and adult individuals are more richly pigmented than *A. akosmos*, with considerable gray and brown dorsally and with dark gray on the ventral surface of the arms (e.g., see Austin and Hadfield, 1980: fig. 10.4). Furthermore, adult *A. occidentalis* consistently have two tentacle scales, ventral arm plates that are distinctly wider than long, dorsal arm plates that are 2.5 to 3 times wider than long, and radial shields that are narrow, not semicircular in shape. There are also marked differences in the reproductive systems of the two species, as noted below.

Juvenile *A. occidentalis* that are equivalent in size to *A. akosmos* are only distinguishable upon microscopic examination (Table 1; Figs. 2, 3). Among their most noticeable differences is that the disk of *A. akosmos* lacks noticeable primary plates and has somewhat larger scales than juvenile *A. occidentalis*

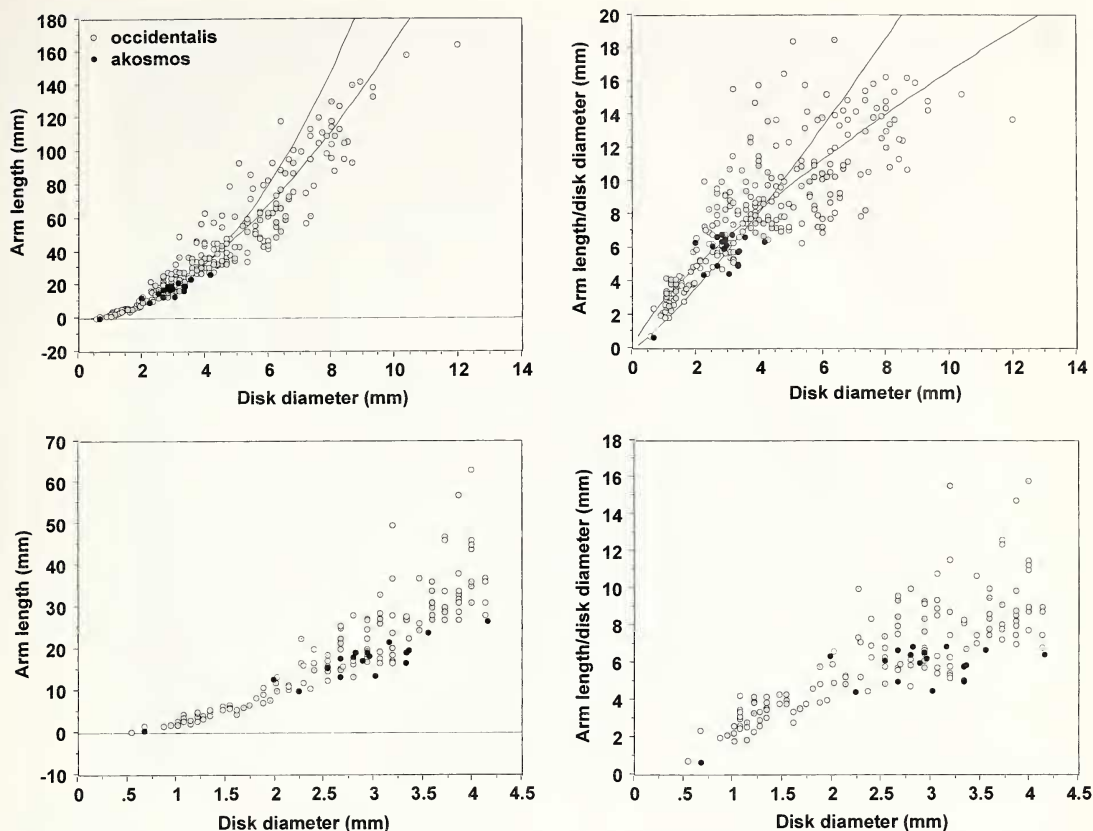


Figure 4 *Amphiodia akosmos* and *Amphiodia occidentalis*. Allometric relationships between the dd and AL (top left) and the AL/dd ratio (top right) for the full size range of the specimens examined. Scatter plots of the relationship between AL and dd (bottom left) and the AL/dd ratio (bottom right) for the specimens in the size range of *A. akosmos* (0.5–4.5 mm dd)

(Fig. 2). Nielsen's (1932) statement that *A. occidentalis* characteristically lacks primary plates is incorrect.

Although individuals of *A. occidentalis* with regenerating disks do not have primary plates, they would not be confused with *A. akosmos* since, as noted during this study, it was only large adult individuals of *A. occidentalis* that had regenerating disks. *Amphiodia akosmos* has considerably more robust arm spines than juveniles of *A. occidentalis*, and its middle spine is noticeably wing-shaped (Fig. 2). In addition, juvenile *A. occidentalis* has zero to two tentacle scales, but *A. akosmos* has a single, markedly elongated tentacle scale and relatively more prominent wedge-shaped scales separating the radial shields.

The possession of a single tentacle scale was previously suggested to distinguish the two species (Weesner, 1954; Sutton, 1975). However, we found that the number of tentacle scales of *A. occidentalis* shifted from zero to one to two in individuals of increasing body size. Those with no tentacle scales

were 0.54 to 3.72 mm dd (1.75 ± 0.73 [$\bar{x} \pm SD$], $N = 71$), those with one tentacle scale were 2.01 to 3.72 mm dd (2.90 ± 0.41 , $N = 31$), and those with two tentacle scales were 2.93 to 11.97 mm dd (5.51 ± 1.73 , $N = 162$). Thus, individuals of *A. akosmos* with one tentacle scale spanned the size range of *A. occidentalis* with zero to two tentacle scales. *Amphiodia akosmos* lacked tentacle scales early in development, as noted for a 0.67-mm dd juvenile, but it appears that Sutton (1975) was mistaken in stating that it can have two tentacle scales. He likely confused *A. akosmos* with juvenile *A. occidentalis*.

Allometric Relationship Between Arm Length and Disk Diameter. The sizes of *A. akosmos* and *A. occidentalis* overlap (Figs. 1, 4), although individuals of *A. occidentalis* can attain a much greater size than *A. akosmos*, up to 12 mm dd and 164 mm AL. Although it had been suggested that the two species are distinguishable on the basis of their size and AL/dd ratio (Weesner, 1954; Sutton, 1975), that is not invariably the case. The AL/dd

Table 2. Relationship between the AL and the AL/dd ratio and dd (body size) of *Amphiodia akosmos* and *Amphiodia occidentalis*. The allometric equation is shown as a power function and in a linearized form.

Species	$Y = aX^b$	$\ln Y = \ln a + b \ln X$	N	r^2	$t(r = 0)$	$t(b = 1)$
<i>A. occidentalis</i>	$AL = 2.909(dd)^{1.756}$	$\ln AL = 1.068 + 1.756(\ln dd)$	264	0.953	72.879*	31.500*
<i>A. occidentalis</i>	$AL/dd = 2.909(dd)^{0.756}$	$\ln AL/dd = 1.068 + 0.756(\ln dd)$	264	0.789	31.292*	-10.160*
<i>A. akosmos</i>	$AL = 1.607(dd)^{2.177}$	$\ln AL = 0.475 + 2.177(\ln dd)$	21	0.917	14.495*	7.846*
<i>A. akosmos</i>	$AL/dd = 1.607(dd)^{1.177}$	$\ln AL/dd = 0.475 + 1.177(\ln dd)$	21	0.764	7.842*	1.180 ns

Abbreviations: b, the constant of allometry; $t(r = 0)$, the calculated value of t in the test for significance of the regression, where H_0 : correlation coefficient = 0 vs. H_A : correlation coefficient $\neq 0$; $t(b = 1)$, the calculated value of t in the test for significant deviations from isometry, where H_0 : constant of allometry = 1 (i.e. isometry) vs. H_A : constant of allometry $\neq 1$ (i.e., allometry); * $P \leq 0.05$; ns, not significant.

ratio of *A. akosmos* examined ranged from 0.69 to 6.89, and the ratio for *A. occidentalis* ranged from 0.74 to 15.79.

For *A. occidentalis* and *A. akosmos*, there was a statistically significant correlation between both AL and AL/dd ratio and body size (dd) (Table 2; Fig. 4). For both species, the coefficient of determination (r^2) for the nonlinear allometric regressions ($Y = aX^b$) exceeded that for linear regressions of the data ($Y = a + bX$). The relationships (except AL/dd vs. dd for *A. akosmos*) were allometric since the hypothesis that $b = 1$ (b = the allometric constant) was rejected (Table 2). For both species, a single ratio of AL/dd is insufficient to characterize either species.

There has been only one comparable examination of the ophiuroid arm allometry, and the results also indicated a positive allometric relationship (López Veléz, 1956). However, the same situation likely prevails in other long-armed ophiuroid species, casting doubt on assumptions in the literature that the ratio between AL and dd is linear and independent of body size.

The AL and AL/dd values for many *A. occidentalis* exceeded those for *A. akosmos* of equivalent disk size (Fig. 4). However, the difference in the values could not be reliably used to distinguish the species because the arm lengths, and AL/dd ratios, of *A. akosmos* and *A. occidentalis* of comparable body size (dd) were overlapping. Analysis of covariance tests of the significance of differences between the regression coefficients of the two species were not warranted, because of departures from normality and heteroscedasticity, even of log-transformed data.

In small individuals, values for AL and AL/dd were depressed compared to those for adults, because the production of arm joints was not initiated until after the disk formed. The smallest *A. akosmos* examined was 0.67 mm dd with AL 0.42 mm. The smallest *A. occidentalis* was 0.54 mm dd with AL 0.4 mm, but another that was 0.67 mm dd already had 1.6-mm arms.

BIOLOGY. Distribution, Habitat, and Associations. *Amphiodia akosmos* has been found at the Great Tide Pool, at Pt. Piños, for the past 25 years

and possibly longer. The population at that locality is protected by an offshore reef at low tides, but subject to considerable wave surge at high tides. The species also has been found nearby at Hopkins Marine Station, where specimens were last collected in 1921; more recently at Waddell Creek, Santa Cruz County, a more southerly site; and offshore in an intertidal cove at Southeastern Farallon Island. It would not be surprising to find *A. akosmos* at other intertidal localities in and beyond the Monterey region if the California and Oregon coastlines were carefully surveyed.

At Pt. Piños, the type locality, *A. akosmos* occurred in low intertidal pools that were exposed at -0.4 ft. (-0.1 m) mean lower low water, and surrounded and protected by algae-draped, granitic boulders. Individuals were found in the shallow layer of sandy sediment beneath and around cobbles and often occurred under the same rocks as *A. occidentalis* and *Amphipholis squamata* (Delle Chiaje, 1828). As an indication of their relative numbers, more than 135 *A. occidentalis* were collected on 23-24 July 1993 in contrast to only seven *A. akosmos*. Occasionally, individuals of *Ophioplocus esmarki* Lyman, 1874, were also found beneath the cobbles, and *Ophiothrix spiculata* Le Conte, 1851, was associated with algae at the type locality.

In 1993, unidentified stalked protozoans were found on *A. occidentalis* in the Great Tide Pool. Some of the preserved specimens of *A. akosmos* collected there at the same time had similar organisms attached to the oral frame and the basal arm spines and tube feet.

Reproduction. *Amphiodia akosmos* broods and may be reproductive for much of the year. Brooding individuals were collected from the Great Tide Pool in May 1975 and February 1976 (Cunningham, 1977). Additional brooding individuals were found in October 1999 and February 2000 (this report). Records of the occurrence and developmental stage of the brooded embryos reinforce the notion that individuals in the Great Tide Pool population do not spawn in synchrony. They also indicate that spawning individuals shed their ripe oocytes at one

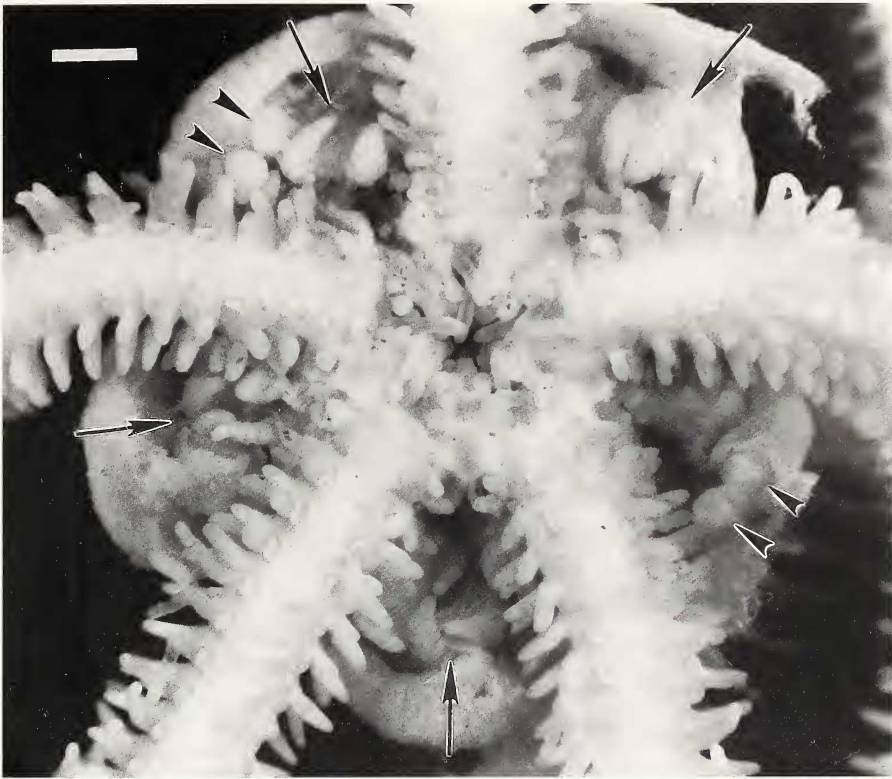


Figure 5 *Amphiodia akosmos*, 4.2 mm dd, LACM 2000-001.002. A brooding individual with interradian sections of the disk wall dissected to reveal embryos with dorsally directed arms (arrows) and pairs of ovaries (arrowheads) within the disk. Scale = 0.5 mm

time, since the embryos in all bursae of brooding females are at the same stage of development.

One specimen of 3.5 mm dd collected in May 1975 was brooding nine embryos, and another specimen collected in October 1999 of 3.0 mm dd contained only one embryo with one to two arm joints. One individual collected in February 2000 was brooding 10 embryos with only terminal arm plates; another was brooding 11 embryos with four to six arm joints (Fig. 5). Both individuals had one to five embryos in each interradius; only one interradius was barren. There were larger oocytes in the ovaries of the individual with larger embryos, indicating that vitellogenesis occurs during brooding.

A single juvenile, with five arm joints, emerged from one brooding female collected in February 2000. It was capable of locomotion using its tube feet and was negatively phototactic (Bundrick, previously unpublished). However, its emergence was probably premature, since the juvenile's disk was still pink and inflated with stored yolk. The brooded embryos in the same female had their arms reflected dorsally, such that their tube feet and mouth were in contact with the bursal wall in a position that may facilitate the uptake of nutrient (Walker

and Lesser, 1989; Byrne, 1994; Hendler and Tran, 2001).

The three individuals collected in October, two in November, and one in December 1999, and two more in February 2000 were dissected; all were female. Thus, the species could be gonochoric, but protandry and parthenogenetic reproduction cannot yet be ruled out without further study. The females had a total of 10 gonads, two within each ventral interradius; additional gonadal tubules were not observed dorsal to the arms (Fig. 5). Each ovary contained approximately one to four oocytes, and individuals appeared to have 30 or fewer pinkish-orange colored oocytes. Most of the oocytes were smaller and contained less yolk than the largest, which was 430 μm in diameter. One *A. akosmos* embryo with a single arm joint was found to have a 400 μm dd. It is likely that it developed from an oocyte of approximately that diameter, since early developmental stages of brooding ophiuroids are often similar in size to the oocytes from which they arise (Hendler, previously unpublished). The low fecundity and the presence of large yolky eggs noted in *A. akosmos* are not unusual traits among brooding ophiuroids (Hendler, 1991).

In contrast to *A. akosmos*, the larger, but morphologically similar, species *A. occidentalis* is a gonochoric broadcast spawner that releases gametes between late May and June in Monterey Bay (Rumrill and Pearse, 1985). Adult individuals were reported to have up to 67,965 yellow-green eggs with a maximum diameter of 90–106 μm , and pelagic larvae (Rumrill and Pearse, 1985; Strathmann and Rumrill, 1987). However, an unpublished study of the species carried out at Friday Harbor, Washington indicated the eggs are orange-pink in color and 190 μm in diameter and that development is benthic, rapid, and direct, producing crawling embryos that hatch from a thick, sticky fertilization envelope (Emlet, personal communication). *Amphiodia occidentalis* was collected from the Great Tide Pool, California, and Pt. Arago, Oregon, in June 1994. The females examined were undergoing oogenesis and had oocytes of mixed sizes. The largest ripe oocytes were pink and approximately 160–192 μm in diameter, consistent with Emlet's observations (Hendler, previously unpublished).

In the previous literature, only one nominal species of *Amphiodia*, *A. affinis* (Studer, 1885), was reported to brood embryos (Mortensen, 1936; Hendler, 1991). Its generic placement is unclear, but it is definitely not an *Amphiodia* (Clark, 1970; Thomas, 1975). Thus, *A. akosmos* presently is the only *Amphiodia* species known to bear live young. It would be unusual among brooding ophiuroids in having separate sexes, if it is indeed gonochoric. Among the approximately 70 known species of brooding ophiuroids only 13 species are gonochoric, but 40 species are hermaphroditic (Hendler, 1991; Hendler and Tran, 2001). The strong association between brooding and hermaphroditism among the ophiuroids remains an enigma (Hendler, 1975, 1991). The brooding mode of reproduction in this and other diminutive ophiuroids may, as previously suggested (Hendler, 1991), offset disadvantages inherent in their small size.

Behavior and Morphology. Adult individuals propel themselves by simultaneously shifting the position of their arms and walking on their tube feet. Individuals quickly retract their arms when disturbed. As it is drawn toward the disk, each arm kinks into sinusoidal waves, which compress into figure eight-shaped loops. Loops at the base of the arm are largest, and those of adjacent arms interdigitate. The five retracted arms form a tightly coiled mass on the dorsal surface of the disk, giving the animal a spherical shape. The behavior is rapid when an individual is wafted into the water column and results in its quickly sinking to the bottom like a pebble. A similar behavior is shown by *A. occidentalis*.

The great morphological similarity of *A. akosmos* and *A. occidentalis*, the direct development of their embryos, and their similar behavior and overlapping ranges, suggest that they are closely related. Certain features of *A. akosmos* give it a juvenile

appearance: its relatively short arms, small number of disk scales, single tentacle scale, narrow arm plates, and broad radial shields. This suggests that it is pedomorphic (as defined by Gould, 1977). However, other traits of *A. akosmos* give it the appearance of a small ophiuroid species with some adult features, and suggest that it is peramorphic. It develops large tentacle scales and conspicuous wedge-shaped scales separating the radial shields at a smaller body size than many individuals of *A. occidentalis*. Moreover, its relatively broad second ventral arm plate is more like those of adult than of juvenile *A. occidentalis*. However, its peculiarly elongated tentacle scale, robust arm spines, and relatively large, opaque, irregularly arranged disk scales differ from the features of both juvenile and adult *A. occidentalis* and may represent adult features or traits that arose *de novo*.

It is tempting to view *A. akosmos* as progenetic—exhibiting precocious sexual maturation and retaining the juvenile characters of its ancestral species. The same mechanism has been proposed as an agent in the evolution of other species of Ophiuroidea (e.g. Matsumoto, 1917; Hendler, 1979; Vadon, 1990). However, assessments of heterochrony require a phylogenetic framework, so that ontogenetic trajectories between ancestral and derived species can be compared. Unfortunately, the necessary framework is lacking in the putative cases of ophiuroid pedomorphosis. Furthermore, as Raff (1996) has emphasized, characteristics that are presumed to be evidence of heterochrony can be the end result of other mechanisms, which are poorly understood. Thus, a better understanding of ontogenetic processes and of phylogeny in *Amphiodia* species are both necessary for a satisfactory appreciation of the evolution in the genus.

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LITERATURE CITED

Austin, W. C. and M. G. Hadfield. 1980. Ophiuroidea: The brittle stars. In *Intertidal invertebrates of California*, eds. R. H. Morris, D. P. Abbott, and E. C.

- Haderlie, 146–159. Stanford, California: Stanford University Press.
- Byrne, M. 1994. Ophiuroidea. In *Microscopic anatomy of invertebrates*, vol. 14 *Echinodermata*, eds. F. W. Harrison and F.-S. Chia, 247–343. New York: Wiley-Liss.
- Clark, A. M. 1970. Notes on the Family Amphiuroidae (Ophiuroidea). *Bulletin of the British Museum (Natural History) Zoology* 19(1):1–81.
- Cunningham, C. J. B. 1977. *Aspects of the reproductive biology of intertidal amphiuroids of Monterey Bay*. Master's thesis, San Jose State University, San Jose, California, viii + 65 pp.
- Friedman, E. 1948. The intertidal ophiuroids of Monterey Bay. Unpublished manuscript. Bodega Bay, California: Cadet Hand Library, Bodega Marine Laboratory, 15 pp., 8 pls.
- Gould, S. J. 1978. *Ontogeny and phylogeny*. Cambridge, Massachusetts: Harvard University Press, 501 pp.
- Hendler, G. 1975. Adaptational significance of the patterns of ophiuroid development. *American Zoologist* 15:691–715.
- . 1978. Development of *Amphiplus abditus* (Verrill) (Echinodermata: Ophiuroidea). II. Description and discussion of ophiuroid skeletal ontogeny and homologies. *Biological Bulletin* 154:79–95.
- . 1979. Sex-reversal and viviparity in *Ophiolepis kieri*, n. sp., with notes on viviparous brittlestars from the Caribbean (Echinodermata: Ophiuroidea). *Proceedings of the Biological Society of Washington* 92:783–795.
- . 1991. Echinodermata: Ophiuroidea. In *Reproduction of marine invertebrates*, vol. 6, *Echinoderms and lophophorates*, eds. A. C. Giese, J. S. Pearse, and V. B. Pearse, 351–511. Pacific Grove, California: Boxwood Press.
- Hendler, G. and L. U. Tran. 2001. Reproductive biology of a deep-sea brittle star *Amphiura carchara* (Echinodermata: Ophiuroidea). *Marine Biology*, 138: 113–123.
- López Vélez, G. 1956. Aplicación de la ley de alometría al estudio de la especie *Ophiactis amphipholoides* Alvarado. *Boletín de la Real Sociedad española de historia natural (Sección Biología)* 54:135–144, 3 graphs.
- Matsumoto, H. 1917. A monograph of Japanese Ophiuroidea, arranged according to a new classification. *Journal of the College of Science, Imperial University of Tokyo* 38:1–408, pls. 1–7.
- Mortensen, T. 1936. Echinoidea and Ophiuroidea. *Discovery Reports* 12:199–348, pls. 1–9.
- Müller, J. and F. H. Troschel. 1843. Neue Beiträge zur Kenntnis der Asteriden. *Archiv für Naturgeschichte* 9:113–136.
- Nielsen, E. 1932. Ophiurans from the Gulf of Panama, California, and the Strait of Georgia. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn*. 91:241–346.
- Raff, R. A. 1996. *The shape of life. Genes, development, and the evolution of animal form*. Chicago: University of Chicago Press, 520 pp.
- Rumrill, S. S. and J. S. Pearse. 1985. Contrasting reproductive periodicities among north-eastern Pacific ophiuroids. In *Echinodermata: Proceedings of the Fifth International Echinoderm Conference*, eds. B. F. Keegan and B. D. S. O'Connor, 633–638. Rotterdam: Balkema.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: The principles and practice of statistics in biological research*. New York: W. H. Freeman, xix + 887 pp.
- Steinbeck, John. 1945. *Cannery Row*. New York: The Viking Press, 208 pp.
- Strathmann, M. F. and S. S. Rumrill. 1987. Phylum Echinodermata, Class Ophiuroidea. In *Reproduction and development of marine invertebrates of the northern Pacific Coast*, ed. M. F. Strathmann, 556–573. Seattle: University of Washington Press.
- Sutton, J. E. 1975. Class Ophiuroidea. In *Light's manual: Intertidal invertebrates of the Central California coast*, eds. R. I. Smith and J. T. Carlton, 627–634. Berkeley, California: University of California Press.
- . 1976. Partial revision of the genus *Amphiodia* Verrill (Ophiuroidea: Amphiuroidae) from the west coast of North America. *Thalassia Jugoslavica* 12: 347–354.
- Thomas, L. P. 1975. The systematic relationships of *Ophioplocus*, *Ophioceramis*, and *Ophioceres* (Echinodermata, Ophiuroidea). *Bulletin of Marine Science* 25:232–247.
- Vadon, C. 1990. *Ophiozonella novaecaledoniae* n. sp. (Ophiuroidea, Echinodermata): Description, ontogeny and phyletic position. *Journal of Natural History* 24:165–179.
- Walker, C. W. and M. P. Lesser. 1989. Nutrition and development of brooded embryos in the brittlestar *Amphipholis squamata*: Do endosymbiotic bacteria play a role? *Marine Biology* 103:519–530.
- Weesner, F. M. 1954. Phylum Echinodermata. In *Intertidal invertebrates of the central California coast*, eds. S. F. Light, R. I. Smith, F. A. Pitelka, D. P. Abbott, and F. M. Weesner, 285–294. Berkeley, California: University of California Press.

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